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Experimental evidence for bird pollination and corolla damage by ants in the short-tubed flowers of *Erica halicacaba* (Ericaceae)

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Abstract

Unrelated plants pollinated by similar animals tend to show convergent evolution of floral traits. Floral syndromes have been used successfully to develop hypotheses about pollination systems but can be misleading when plants have unusual floral morphology or mechanisms of pollen transfer. A case in point is *Erica halicacaba,* a local endemic shrub on the Cape Peninsula of South Africa. Its short-tubed greenish-yellowish flowers with a narrow aperture have been considered to be insect pollinated. However, field observations, selective exclusion experiments and analysis of pollen loads all indicate that its primary pollinator is the Orange-breasted Sunbird (*Anthobaphes violacea*). These sunbirds were common visitors and netted individuals carried large numbers of *E. halicacaba* pollen tetrads on their culmens, rather than on their head plumage as is typical for Cape *Erica* species with longer tubular flowers. Plants of *E. halicacaba* from which vertebrates were excluded had a lower incidence of anther tripping and set significantly fewer seeds than those exposed to both birds and insect visitors. Nectar in *E. halicacaba* is present in small concentrated amounts and, typical of sunbird-pollinated plants, is dominated by sucrose. Flowers often had holes in their corollas and we identified ants, specifically *Myrmicaria nigra*, as the likely agents. This was supported by reduced rates of corolla damage on branches from which crawling insects such as ants were experimentally excluded. These findings indicate that considerable caution should be applied when attempting to predict pollinators from floral syndromes, and highlight the role that crawling insects can play in damaging flowers.

Keywords: *Anthobaphes violacea*; Bird pollination; *Erica halicacaba*; Ericaceae; Floral Syndromes; Nectar Robbing; Nectar; Pollination Biology

1. Introduction

The concept of floral syndromes can be traced to Kölreuter's (1761) descriptions of plant-pollinator interactions and floral morphology (Fenster et al., 2004). It has been controversial on account of its association with a typological school of pollination biology that was not grounded in evolutionary biology, and because there has been uncertainty about the degree of specificity in pollination systems (Johnson and Steiner, 2000; Pauw, 2006; Waser et al., 1996). Fenster et al. (2004) defined a floral syndrome as "a suite of floral traits, including rewards, associated with the attraction and utilization of a specific group of animals as pollinators", and further emphasised the importance of classifying pollinators into functional groups according to the selective pressures they exerted, as these typically influence evolution of suites of floral traits. It is in this sense that Hargreaves et al. (2004) proposed that "floral syndromes can be seen as patterns of convergent evolution that are useful for developing testable hypotheses about pollination systems".

Workers have emphasised the usefulness of floral syndromes (De Merxem et al., 2009; Hargreaves et al., 2004; Pauw, 2006) and it is a feature of many pollination studies that pollinators are initially inferred from the floral morphology

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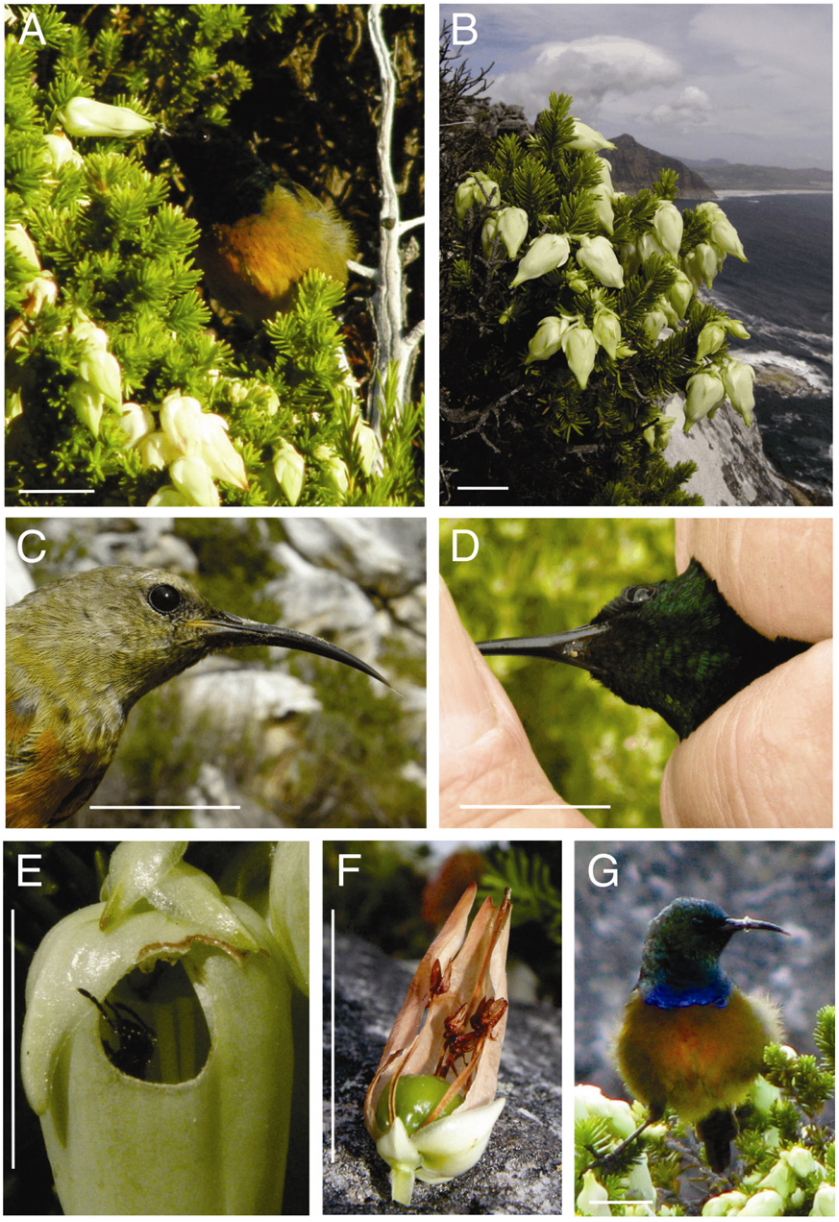

Fig. 1. (A) *Anthobaphes violacea* pollinating *E. halicacaba*. Scale 20 mm. (B) *Erica halicacaba* in typical habitat. Scale 20 mm. (C) Pollen on culmen of juvenile Orange-breasted Sunbird. Scale 20 mm. (D) Scalloped area on underside of culmen with pollen amalgam. Scale 20 mm. (E) *Myrmicaria nigra* causing floral damage to an *E. halicacaba* flower. Scale 10 mm. (F) Fertilised flower. Scale 20 mm. (G) Male visitor with pollen on culmen. Scale 20 mm. All photos R.C. Turner, except (G) Rob Simmons.

of plants (e.g. Kleizen et al., 2008; Manning and Goldblatt, 2005; Turner et al., 2011). In the majority of these studies, predictions have been confirmed by later observation, thus the predictive value of floral syndromes can be high. However, the utility of floral syndromes has been questioned (Ollerton et al., 2009) and several studies have demonstrated that there are limits to the power of predictive paradigms, especially in specialised single-pollinator mutualisms (Castellanos et al., 2003; De Merxem et al., 2009; Johnson, 1995; Olesen and Valido, 2003; Pauw, 1998). A case in point is Pauw's (1998) study of bird-pollinated in *Microloma sagittatum* (L.) R.Br. (Apocynaceae), a species which possesses some traits consistent with bird-pollination, such as the firm-textured, unscented, tubular, red flowers with accessible perching posts, but, also traits usually associated with insect pollination, such as a short floral tube with a narrow entrance. Ollerton (1998) noted that these traits had "excluded *M. sagittatum* from being recognized as a bird-pollinated plant — these characteristics did not fit preconceived ideas of what such a plant should look like". Similarly, de Merxem et al. (2009) concluded their study of variable flower tube length in *Tritoniopsis revoluta* (Burm.f.) Goldblatt by commenting that "although syndromes may provide clues about prospective pollinators, they are not always a fail-safe way of predicting all of a flowers' important visitors".

Bird-pollinated flowers typically have brightly coloured flowers, often red, orange and sometimes pink (Anderson,

2005; Johnson, 1995; Manning and Goldblatt, 2005; Pauw, 1998). The question of why so many bird-pollinated flowers are red has been explored by Raven (1972) and more recently reviewed by Rodríguez-Gironés and Santamaría (2004), who focussed upon the energetics of, and competition between, pollinator guilds to explain why red flowers were favoured by birds and purple flowers by bees. They emphasised that certain bee species can see the red end of the light spectrum and that birds can detect purple flowers, and that an explanation could therefore not be as simple as "bees can't see the colour red". The Cape flora contains numerous examples of tubular *Erica* species with brightly-coloured, red, pink, white, orange, yellow and green flowers, with approximately 50% of putatively bird-pollinated species having more than two colour forms, and in several cases, bicoloured and tricoloured forms (Oliver and Oliver, 2002; Rebelo et al., 1985). A noteworthy example is *Erica viscaria* L. subsp. *viscaria*, which has flowers "12–20 mm-long, tubular, non-viscid, hairy or postulate, red, pink, purple, white, yellowish or green, in some cases bicoloured - pink with a white mouth or red with a yellow mouth" (Oliver and Oliver, 2002). While Rebelo et al. (1985) concluded that the Orange-breasted Sunbird was the sole pollinator of ornithophilous Cape *Erica* species, recent studies by Geerts and Pauw (2009, 2010) have shown that Southern Double-collared Sunbirds (*Cinnyris chalybea*) visit flowers of *Erica cruenta* Sol., *Erica discolor* Andrews and *Erica perspicua* Wendl., suggesting that it is not only one specialist passerine nectarivore that has imposed selective pressure upon bird-pollinated Cape *Erica* species.

Baker and Baker (1983, 1990) proposed that hummingbirds and passerines such as sunbirds select for different nectar properties in the flowers they pollinated. Johnson and Nicolson (2008) suggested that a more useful paradigm involved grouping birds into subcategories of specialist and generalist pollinators. They reported that flowers adapted for pollination by specialized passerine nectarivores, whether hummingbirds or sunbirds, typically had small amounts of sucrose-rich nectar, and that flowers adapted for generalist bird pollinators typically had large amounts of dilute nectar with very low sucrose content. Barnes et al. (1995) showed that 29 of the 37 ornithophilous *Erica* species they studied had sucrose-dominant nectars with a mean sucrose proportion of 93.8±6.2% (mean±SD). As their results were not consistent with the original ideas of the Bakers, they concluded that pollination syndromes could not be deduced from nectar types. However, their finding of sucrose-dominated nectar in *Erica* is actually consistent with the more recent finding that plants pollinated by specialized passerine nectarivores tend to have sucrose-dominated nectar (Johnson and Nicolson, 2008).

The floral morphology of *Erica halicacaba* L. (Fig. 1) is unique within the genus *Erica* because of its gooseberry-shaped flowers (*halicacaba*=gooseberry. Gr.) with adpressed lobes and its pollinator has been unknown since the taxon was described by Linnaeus in 1760. Rebelo et al. (1985) categorised 426 south-western Cape *Erica* species "according to their principal putative pollinating agents, based on the shape of the flowers and field observations", suggesting the possibility of bird pollination in *E. halicacaba* (p. 276), although they subsequently classified the species as insect pollinated in the same paper (p. 279). Their suggestion was that large flying hymenopterans, e.g. carpenter bees, could reliably pollinate flowers by forcing open the adpressed corolla lobes. Based on observations of cultivated *E. halicacaba* plants at the Kirstenbosch National Botanical Garden, Rebelo et al. (1985) observed that bees chewed holes in the bases of corollas in order to rob nectar, and Oliver and Oliver (2000) suggested that the large flowers may serve as an "overnight or cool weather shelter" for insects, presumably resulting in fertilization of flowers. However, preliminary field observations of Orange-breasted Sunbirds (*Anthobaphes violacea*) visiting flowers of *E halicacaba* led us to hypothesize that this species, which is a member of a guild of at least ten *Erica* species with similar short-tubular, yellow to greenish-yellow flowers, is specialized for pollination by sunbirds.

2. Materials and methods

2.1. Study site

Field studies took place during October and November of 2009 on Glen Cairn Ridge, southern Cape Peninsula, South Africa (34.147136S, 18.427021E; 190 m). Approximately 250 mature plants were available for study purposes. As pollen tetrads of *E. halicacaba* could potentially be confused with those of other *Erica* species, we checked the study site for other co-flowering *Erica* species and Cape taxa known to have pollen in tetrads.

2.2. Study taxon

Erica halicacaba is endemic to the Cape Peninsula (South Africa, Western Cape), occurring on rocky ridges and mountain tops from Table Mountain to Paulsberg in the Cape of Good Hope Nature Reserve. In rockier fire refugia individual plants may attain heights of more than 2 m tall, with gnarled, woody trunks more than 0.15 m in diameter, or form mats up to 2 m^2 in area on vertical cliffs. Plants are generally floriferous, mature individuals bearing many hundreds to thousands of gooseberry-shaped, greenish-yellow flowers with a mean corolla length of 22.5 mm (20.0–24.5 mm; n=25). Peak flowering occurs from July to November and is variable between localities, depending on aspect, habitat and microclimate. Far more than 2000 plants occur in at least 20 locations and the species is classified as a taxon of least concern (LC) in the 2010 IUCN South African Red Data Plant List (Raimondo et al., 2009).

2.3. Pollinator observations and bird mist netting

We observed pollinator-plant interactions during the early morning (6–10 am) and late afternoon (4–8 pm) for 12 days, from 19 to 30 November 2009.

Birds were netted on 26 November 2009, using Ecotone 12 m, 5-shelf nylon mist-nets with 16 mm mesh. Nets were positioned approximately 30 m from our observation point, a rocky outcrop containing multiple mature *E. halicacaba* individuals. Mist nets were constantly monitored for bird-captures by three fieldworkers for a period of approximately 4 h.

Culmens were swabbed for pollen using sections of double-sided adhesive tape ± 5 cm long. The non-adhesive protective backing covering the adhesive surface used for sampling was replaced after culmen swabbing. Netted birds were immediately swabbed while still in mist nets and then disentangled for collection of biometric data and ringing. Individual birds were released less than 10 min after initial capture. Pollen swabs were examined in the laboratory at 45–60 × magnification under a Vickers Light Stereoscopic microscope. Pollen grains were identified and counted.

2.4. Selective exclusion experiments

To determine whether birds were important for seed production in *E. halicacaba*, and also whether plants were capable of autonomous seed production, we selectively excluded either vertebrates only or all flower visitors. This was done on 10 separate mature plants at different localities within the population. Selective exclusion of vertebrates was achieved by covering flowering branches with wire "chicken-mesh" exclosures (mesh aperture ± 15 × 17 mm), and exclusion of all visitors was achieved with bridal veil exclosures (aperture ± 0.8 mm diam.). Uncovered inflorescences were used as controls. Treated inflorescences were examined one month later to assess rates of visitation and seed set. Visitation to flowers of many *Erica* species, including *E. halicacaba,* is easily scored by determining if the anther rings have been tripped (Geerts and Pauw, 2010; Turner et al., 2011). Mature, unvisited flowers have an untripped anther ring, i.e. adjacent anther thecae remain connected laterally. When manipulated, anther rings break (are triggered) and pollen is visibly ejected from apical anther pores. Visits by Orange-breasted Sunbirds, as observed in the field during this study, result in tripped anther rings. Seed set was established by dissection of fruits. Developing seeds are distinguishable from ovules by their larger size and "honey-combed" testa.

The effects of selective exclosure on the proportion of flowers on each treated branch that had tripped anthers or which developed fruits was analyzed using generalized linear models with a binomial error distribution, implemented in PASW Statistics 18 (SPSS, Chicago, USA). Plant was used as a blocking factor and was entered in the model before treatment. Model significance was assessed using likelihood ratio tests and posthoc pairwise comparisons of means were conducted using the Šidák procedure. Mean proportions and asymmetrical standard errors were obtained by back-transformation from the logit scale.

2.5. Role of crawling insects in corolla damage

Preliminary observations suggested that damage to flowers in the form of holes pierced in corollas was effected by ants. Specimens of the ant species observed to be commonly responsible for corolla damage were collected for identification at the Iziko Museum, Cape Town. To assess the frequency of corolla damage by ants, the mean percentage of flowers per branch experiencing active corolla damage by ants (ants active around holes in the corolla) was calculated for the mature flowers on 10 branches on 10 randomly chosen plants throughout the population.

To determine if holes in the corolla were made by flying insects, such as bees, as was suggested by Rebelo et al. (1985), or by crawling insects, such as ants, sticky Plantex® was applied around the stems of ten freestanding flowering branches on ten separate plants throughout the population to exclude all crawling insects. Flowers were examined one week later to quantify floral damage in the form of holes in corollas. Untreated branches on the same plants were used as controls. The proportion of flowers robbed for the two groups was analyzed using generalized linear models with a binomial error distribution. Plant was used as a blocking factor and was entered in the model before treatment. Model significance was assessed using likelihood ratio tests. Mean proportions and asymmetrical standard errors were obtained by back-transformation from the logit scale.

2.6. Nectar properties

Nectar was sampled from 114 flowers from 114 separate plants throughout the population, using disposable, calibrated 1 ml micro-syringes. Nectar sugar concentrations were measured using two Eclipse handheld refractometers (Bellingham and Stanley Ltd.), one capable of taking measurements of up to 50% and the other up to 80% sugar concentration. Nectar sampling took place between 7 am and midday. Individual nectar samples were stored in separate eppendorfs, and four of these samples later spotted onto four 7.0 cm Whatman filter papers and dried for later determination of constituent free sugars using HPLC methods, as described by Brown et al. (2009).

3. Results

3.1. Pollinator observations

Birds thoroughly "worked" plants of *E. halicacaba*, often concealed within the well-branched shrubs for up to 30 min while visiting flowers. Movement from one plant to another was observed during all fieldwork periods. Birds used the sturdy main and side-branches, as well as flowers, as perches. Birds approached flowers from above, below and side-on, manipulating individual flowers, which are attached to the plant by a robust pedicel (±3 mm long and 1 mm diam.). Birds were not observed to rob flowers by piercing holes in corollas. Pollen placement was on the lower third of the culmen (Fig. 1C) and also in a small depression at the base on the underside of the lower culmen (Fig. 1D).

Fourteen *A. violacea* individuals were netted on 26th November 2009. All fourteen birds had *E. halicacaba* pollen tetrads on their culmens and the mean number of pollen tetrads per bird sampled was 79 (range 20–200). The tetrads were assumed to be from *E. halicacaba* since no other *Erica* species were flowering on Glen Cairn Ridge at that time, and as the three other Cape genera known to have pollen tetrads were likewise absent, viz. *Typha capensis* (Rohrb.) N.E.Br. (Typhaceae), *Cytinus*

sanguineus (Thunb.) Fourc. (Cytinaceae), and *Drosera capensis* L. (Droseraceae) (Copenhaver, 2005). Pollen from only one other plant species was recorded on all of the 14 culmens: yellow monads of *Saltera sarcocolla* (L.) Bullock.

3.2. Selective exclusion experiments

Selective exclosure of flowering branches significantly decreased the frequency of flowers with tripped anther rings (χ^2=274.1, df=2, P=< 0.001; Fig. 2A). Each treatment was also significantly different, indicating a strong effect of the exclosures on rates of pollinator visitation. Thus 91.5% of open inflorescences (controls) had flowers with tripped anther rings; 31.7% of flowers in the chicken wire treatment group had tripped anther rings, birds presumably occasionally managing to penetrate chicken wire exclosures; but only 1.5% of flowers in the bridal veil treatment (all visitors excluded) had tripped anther rings (these may have been disturbed when the exclosure was applied) and only 0.7% of flowers (2 flowers) set seed. Thrips were observed in several individual flowers but owing to their small size (< 2 mm long and<0.5 mm wide) (Picker et al., 2004) they are not capable of displacing anther rings of the larger southern African *Erica* species (Turner et al., 2011), especially those of the robust-flowered *E. halicacaba*.

Selective exclosure of flowering branches had a similar negative effect on the frequency of flowers that set seed (χ^2=287.1, df=2, P<0.0001; Fig. 2B) and all treatments were significantly different. Seed set occurred in 87.1% of open controls; in 17.2% of vertebrate-excluded flowers; and in 0.01% of the flowers from which all visitors were excluded.

3.3. Role of crawling insects in corolla damage

No visits by flying insects, such as *Apis mellifera* L. (Hymenoptera), carpenter bees (*Xylocopa* spp., Hymenoptera), or blister beetles (Meloidae), were observed during this study (± 96 hours). The main ant species observed to be responsible for corolla damage was identified as *Myrmicaria nigra* Mayr at the Iziko Museum, Cape Town. *M. nigra* was observed to damage flowers of *E. halicacaba* by chewing holes on the corolla throughout the study population, during all fieldwork periods. Tiny bird claw puncture holes in corollas, as a result of perching, are enlarged and exploited by *M. nigra* in order to rob nectar. The mean (± SD) percentage of flowers actively robbed by ants was 65±5.0.

Floral damage by crawling insects was significantly reduced by application of Plantex® to freestanding branches (χ^2=146.1, df=1, p <0.0001). The mean percentage of flowers pierced was 1.0 (lower se: 0.66; upper se: 1.36) for Plantex® treated plants versus 64.1 (lower se: 4.86; upper se 4.59) for control plants.

3.4. Nectar properties

The mean (± SD) nectar standing crop volume was 12.0± 21.0 μl (range 1.25–100 μl). The mean (± SD) nectar sugar concentration was 36.4±11.9% (range 19–63.5%). The nectar was sucrose-rich, with sucrose (55.55±1.2%), glucose (17.2± 0.4%) and fructose (25.8±0.6%).

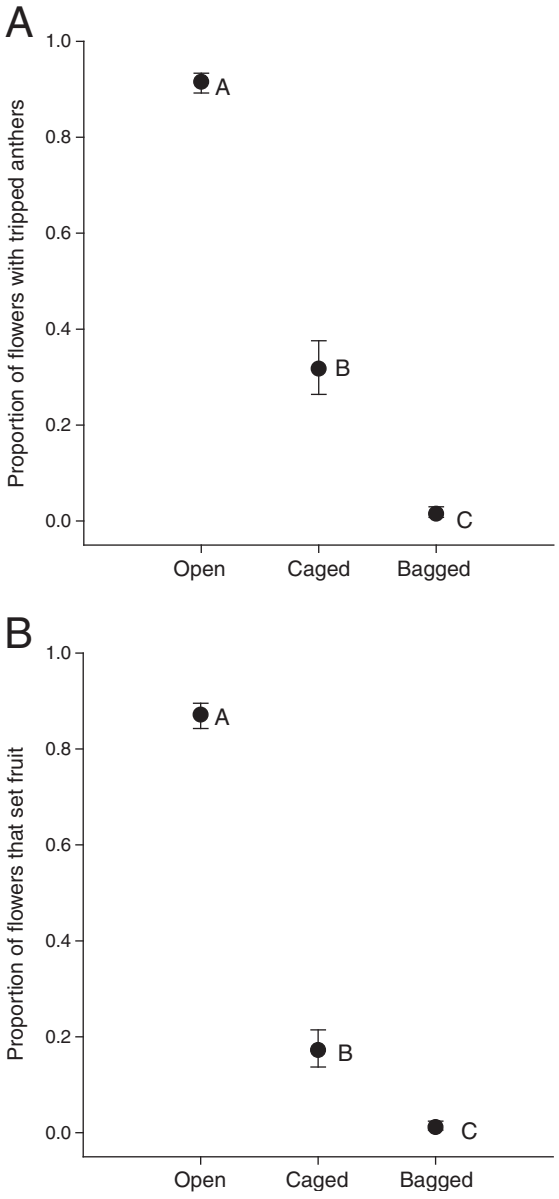

Fig. 2. The effects of selective exclusion experiments on anther tripping (A) and fruit set (B) in *Erica halicacaba*. Values are back-transformed means and standard errors. Means that have different capital letters are significantly different.

4. Discussion

Data supporting the hypothesis that flowers of *E. halicacaba* are adapted for pollination by Orange-breasted Sunbirds include repeated observation of legitimate pollination behaviour with no observed robbery by birds; large numbers of pollen tetrads recorded on culmens of all mist-netted birds; high visitation rates and seed set in open control flowers versus vertebrate-excluded and bridal veil exclosures; and small volumes of sucrose-rich nectar consistent with trends in other flowers pollinated by sunbirds (Johnson and Nicolson, 2008).

We showed experimentally that floral damage could be reduced to negligible levels (1% as opposed to 64.1% in open controls) by application of Plantex® to exclude crawling floral predators, including *Myrmicaria nigra* ants, which we observed and recorded to be responsible for extensive damage of flowers in the wild (Fig. 1E). Ants are known nectar robbers (Fritz and Morse, 1981; Haber et al., 1981; Herrera et al., 1984) and as such, may have neutral or negative effects on plant fitness, influence floral evolution, have impacts upon plant population demographics, and influence the stability of established mutualisms (Irwin et al., 2001). In particular, Irwin and Brody (1998) found that hummingbirds visited significantly fewer plants in which "heavy" experimental robbing treatments had been performed. While we did not study the impact of floral damage upon visitation and seed set, open control treatments showed high visitation and pollination rates by *A. violacea* despite presence of and damage by ants, suggesting that ants do not alter the visitation dynamics of *A. violacea* to flowers of *E. halicacaba*. Furthermore, while corolla damage by ants was significant in our study population, the stochastic nature of floral robber-plant interactions (cf. Irwin and Brody, 1998) are such that the *ex situ* observations by Rebelo et al. (1985) of bees as floral robbers may well hold for other populations of *E. halicacaba* on the Cape Peninsula. Nevertheless, our study shows that ants can cause extensive damage to the flowers of Cape plants.

Geerts and Pauw (2009) emphasised the correlation between culmen length and flower length in "short-" and "long-billed" sunbird pollination syndromes. Mean corolla lengths of *E. halicacaba* and *S. sarcocolla* flowers are 22.5 mm (n=25) and 23.5 mm (15–28 mm; n=25) respectively, which correspond with reported *A. violacea* culmen lengths of 20–23 mm (Rebelo, 1987, in Geerts and Pauw, 2009). Geerts and Pauw (2009) also reported that short-billed sunbirds showed a tendency to rob longer tubular flowers for which their culmen length was too short. Our observations of zero robbery of *E. halicacaba* flowers by *A. violacea* suggest that no mismatch of plant-pollinator morphology exists within the mutualism (de Merxem et al., 2009).

In our study, pollen was deposited on the lower third of culmens in all 14 netted birds (Fig. 1C). To reach nectar without robbing, a bird could only enter through the adpressed corolla lobes, tripping the anther ring in the process. This is in contrast to pollination syndromes of hummingbird-pollinated flowers (Castellanos et al., 2003), and to longer-tubed Cape *Erica* and other species in which pollen is typically placed on the head plumage of visiting birds (Geerts and Pauw, 2009; Johnson, 1995; Manning and Goldblatt, 2005). Of further interest concerning pollen placement is the small depressed area at the base of the underside of the lower culmen (Fig. 1D): here we regularly (64% of netted birds) recorded an amalgam of white *E. halicacaba* and yellow *S. sarcocolla* pollen grains. Owing to the adpressed corolla lobes, repeated visits by birds to flowers result in pollen loads from previous visits being pushed towards the base of the bill, where they collect in the excavated area. Hummingbird-pollination of short-tubed, urn-shaped flowers of Brazilian Ericaceae also involves pollen placement on the culmens of birds (Freitas et al., 2006). In the light of the very few flowering bird-pollinated plant species on Glen Cairn ridge during October and November, as well as our records of only two pollen types on culmens of mist-netted birds, we can deduce that the nectar of *E. halicacaba* and *S. sarcocolla* were an important energy source for resident Orange-breasted Sunbirds at that time.

We conclude that experimental field data and *in situ* observation have been important in determining both the pollination system of *E. halicacaba*, as well as the contribution of crawling insects, especially ants, to flower damage.

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